

# Resilience of Microbial Systems Towards Disturbances

**S. Botton\***

*Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, The Netherlands*

**M. van Heusden\***

*Laboratory of Microbiology, Wageningen University, The Netherlands*

**J. R. Parsons**

*Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, The Netherlands*

**H. Smidt**

*Laboratory of Microbiology, Wageningen University, The Netherlands*

**N. van Straalen**

*Institute of Ecological Science, Free University Amsterdam, The Netherlands*

---

**In this paper we aim at summarizing the current definitions of resilience in systems ecology with particular attention towards microbial systems. The recent advances of biomolecular techniques have provided scientists with new tools to investigate these systems in greater detail and with higher resolution. Therefore existing concepts and hypotheses have been revisited and discussed with respect to their applicability for ecosystems ruled by microbial processes. This review has also led to some reflections on the suitability of the term “resilience” as a general goal in environmental policies.**

---

**Keywords** Resilience in Systems Ecology; Microbial Systems; Ecosystems; Environmental Policies

## INTRODUCTION

Currently, the term resilience is frequently used in the framework of environmental protection strategies. Especially in the case of subsoil and groundwater ecosystems management, the use of resilience has gained in popularity although only few studies have investigated resilience in those systems and the consensus on parameters that can or should be used for a proper evaluation has not been reached yet.

A review of the literature of the last decade shows that the concept of resilience in systems ecology has been applied in numerous studies over the past fifty years: a variety of defini-

tions have been formulated and a large number of experimental approaches to test them have been proposed. In contrast, only a few studies have investigated the resilience of subsoil and groundwater ecosystems including the microbial community structure and function. Moreover, the necessary simplification required to approach such studies has inevitably brought one to “collapse” the microbial community into one (bacteria) or few functional groups (for example, nitrogen fixers, decomposers, methanogens) and very few studies have described stability and resilience in a solely microbial ecosystem.

While scientists are developing new tools and applying novel methodologies to study these systems at different scales and resolution, environmental policymakers and managers should be aware of gaps and open questions in theories and adopt the term “resilience” with caution, without confusing it with generally accepted and well defined concepts like biodegradation or natural attenuation. The ability of groundwater ecosystems to decrease the concentration of a pollutant in the environment is referred to as natural attenuation, and biodegradation (biological transformation of a compound) is one of the processes with which pollutants can be removed. These two concepts have clear positive connotations and, in case of a polluted environment, are desirable. Resilience is an ecological term that defines the ability of a system to react to a certain perturbation, as described in the following paragraph, but is not necessarily a positive concept: a polluted system can be very resilient to change, for example towards active remediation or the introduction of bacteria able to degrade that specific contaminant, and as a consequence it might be very difficult to modify it. Whether or not high resilience is good therefore depends upon the system under investigation.

---

\*Both authors contributed equally.

Address correspondence to S. Botton, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, The Netherlands. E-mail: sbotton@science.uva.nl

The advent of new approaches, independent of cultivation and amenable to high-throughput analyses of a large number of samples, at high temporal and spatial resolution, urges us to revisit existing concepts and hypotheses and discuss their applicability to ecosystems ruled by microbial processes. With this review we aim at revisiting the existing ecological concepts and hypotheses in order to provide a non ecologist reader with sufficient background to further discuss the concept of resilience in real field conditions, to evaluate the difficulties that are still unsolved and the applicability of this concept in environmental protection strategies of ecosystems ruled by microbial processes.

## Definition

The etymology of the word “resilience” derives from the Latin “resilire” which means “to spring back” or “rebound” and is described as springiness or elasticity (<http://www.biology-online.org/dictionary.asp>). In general terms, it is a word used to denote the dynamic feature of a system. It has been first adopted in physics (as the energy per unit volume absorbed by a material when it is subjected to strain, or the maximum value of this at which the elastic limit is not exceeded) (Grime 2003). Resilience can also be found in the field of psychology where it has been defined as the ability “to overcome the odds and achieve better than expected, to adapt in spite of stressful experiences and to recover from a single traumatic experience” (Waller 2001; Johnson & Wiechelt 2004).

In ecology various definitions have been used to suit the scale or the system that was under investigation: narrowing the definition makes it, from a practical perspective, more suitable to work with. However, such a reductionistic approach makes it more difficult to find and support one central theory in ecology (Loreau et al. 2001; Ulanowicz 2003).

## Resilience and Stability in Ecological Literature

A milestone with respect to the application of the resilience concept to ecosystems is represented by the early work of Holling who, in 1973, proposed that the behavior of ecological systems should be defined by two distinct properties, resilience and stability, where “Resilience determines the persistence of relationships within a system and is a measure of the ability of these systems to absorb changes and still persist. In this definition, resilience is the property of the system and persistence or probability of extinction is the result.

Stability, on the other hand, is the ability of a system to return to an equilibrium state after a temporary disturbance. The more rapidly it returns, and with the least fluctuation, the more stable it is. In this definition stability is the property and the degree of fluctuation around a specific state the result” (Holling 1973). One important realization is therefore that, in an ecological sense, resilience and stability are concepts that cannot be separated (DeAngelis 1980; DeAngelis et al. 1989; McCann

2000). As a matter of fact, the concept of stability in ecological systems was already described by Darwin and MacArthur. Darwin in 1859 proposed that an area is more ecologically stable if it is occupied by a large number of species, and similarly MacArthur earlier suggested that the addition of species stabilizes an ecosystem by increasing the number of ecological functions present (MacArthur 1955).

Later in 1968 Margalef defined the stability of a system as its ability to return to a state reasonably close to its original state in the presence of perturbations (Walter 1980).

The use of the term “resilience” in ecological studies first appeared in the late 1950s and referred to the amplitude of changes brought about by disturbance and the dynamics of post disturbance recovery (Elton 1958).

A comparison of these early definitions suggests that they are prone to confusion. Therefore in 1996 Holling proposed that the concept of ecosystem stability does actually present two contrasting aspects: one that focuses on maintaining efficiency of functions, which corresponds to engineering resilience, and one that focuses on maintaining existence of function which was named ecological resilience (Holling 1996a).

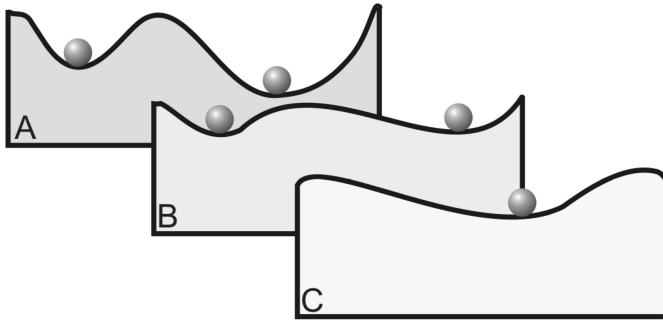
Most of the existing definitions can also be grouped under these two concepts.

The concept of engineering resilience assumes the existence of global stability: only one equilibrium steady state exists, or, if other operating states exist, they should be avoided by applying safeguards (Holling 1996a). Consequently, even if several steady states can occur, resilience has meaning only for locally stable systems, and, moreover, only in closed systems and for perturbations that redistribute matter within a given system (DeAngelis et al. 1989). Engineering resilience, as defined by Holling, concentrates on stability near an equilibrium steady state, where resistance to disturbance and speed or time of return to the equilibrium are used to measure the property (Holling 1973; DeAngelis 1980; DeAngelis et al. 1989; Tilman and Downing 1994; Griffiths et al. 2000; McCann 2000; Ulanowicz 2003).

In terms of stability landscapes, as depicted in Figure 1, the engineering resilience refers to characteristics of the shape of the cup, while the slope of the sides dictates the return time of the ball to the bottom or the equilibrium (Gunderson 2000).

The second definition, ecological resilience, emphasises conditions far from the equilibrium steady state, where instabilities can flip a system into another regime of behavior—that is, to another stability domain (Holling 1973). In this case the measurement of resilience is the magnitude of disturbance that can be absorbed before the system changes its structure by changing the variables and processes that control behavior. This concept can be visually represented by the width of the stability domain, or valley (Figure 1).

Ecological change is not continuous and gradual and structural instabilities are common in ecosystem models. Continuous changes in the level of nutrient input can lead to discontinuous changes in community structure: it allows new species



**FIG. 1.** Ball and cup heuristic of system stability. Valleys represent stability domains and balls represent the system. Engineering resilience is determined by the slopes in the stability landscapes, whereas ecological resilience is described as the width. Disturbances would be pushing the system up the slope. If resilience is high (A) much bigger disturbances would be needed to push the system into another attraction domain and the speed of return to equilibrium is higher. Ecological change may modify the shape of the domain and decrease system resilience (B) or move the system to another equilibrium point (C). Adaptive capacity refers to the ability of the system to remain in a stability domain, as the shape of the domain changes (as shown by the three slices or landscapes) (Gunderson 2000).

on higher trophic levels to successfully invade; it changes the balance between competing species, causing sudden replacement of some species by others (DeAngelis et al. 1989; Holling 1996b; Ulanowicz 2003). Because several stability domains can exist, the main focus is on keeping the ecosystem within some bounds rather than at a stable point (Walter 1980; Holling 1996a; Häggblom et al. 2000; Bengtsson 2002).

It is important to note that the stability and resilience concept can be applied to two distinct components of an ecosystem: the structural biotic component (communities) and the process component (the flow of matter or energy among the functional compartments). The stability of each of these components is usually not related and for example microbial communities with greater stability of diversity would, paradoxically, have less stability of function because of a lower functional redundancy (Fernandez et al. 1999; Fernandez et al. 2000; Hashsham et al. 2000; Briones & Raskin 2003). Also within the ecological definition of resilience the focus can be towards the process component of the system or towards the biotic component, where often the (probability of) persistence of species is used as a determinant of stability (Walter 1980; DeAngelis et al. 1989; Walker 1995; Lal 1997; Lynch 2002).

When including a factor of learning and adaptation in the concept of resilience, several authors have applied the term “socio-ecological” resilience. Carpenter et al. described it as being related to the magnitude of shock that the system can absorb and remain within a given state, the degree to which the system is capable of self-organization and the degree to which the system can build capacity for learning and adaptation (Carpenter et al. 2001). In short, socio-ecological resilience is the capacity to buffer change, learn and develop and reorganize while undergoing change so as to retain essentially the same function,

structure, identity, and feedbacks (Folke et al. 2002; Folke et al. 2004). Adaptive capacity is a term for a broad class of flexible learning responses (Walker et al. 2002).

## ECOLOGICAL THEORY

How can resilience be measured? To approach this question, hypotheses (or models) have to be formulated in order to link the very definition of resilience with the experimental observations.

One of the first hypotheses was already considered by Darwin in 1859. He linked species richness to ecosystem resilience by proposing that ecological stability increases with an increasing number of species. The link between species diversity and resilience has been one of the most popular theories and gave rise to several (sometimes competing) models. A step forward was the recognition that species function rather than number was more relevant, and based on this assumption other theories like the redundancy and insurance hypothesis were developed.

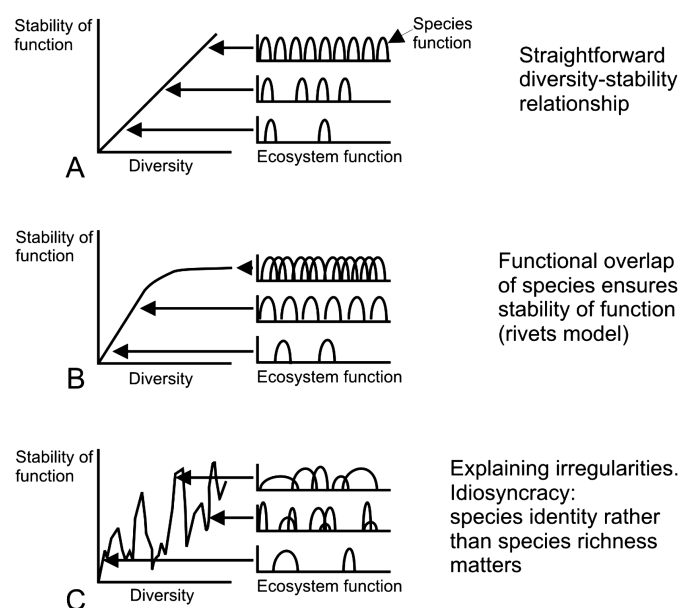
The observation that different responses can occur within similar environments was the trigger for additional theories such as niche differentiation, complementarity, sampling effect, and idiosyncrasy. These theories, for which species diversity is the main driver, were complemented by others that suggested a link between fluxes of nutrients or energy through a system and its resilience. Both diversity and fluxes can be found combined in food web models, where in some cases the diversity issue has been drawn away from the pure species richness concept towards functional diversity or even diversity of possible interactions.

## Species Diversity

Darwin’s idea of ecological stability was formalized by MacArthur, who proposed that the addition of species to an ecosystem increases the number of ecological functions present and that this increase stabilizes an ecosystem (Figure 2a) (Peterson et al. 1998). Many examples have been found in which resilience and increasing species richness were positively correlated.

Initial research claimed to demonstrate benefits to ecosystem function from higher biodiversity (Tilman & Downing 1994; Naeem & Li 1998; Griffiths et al. 2000; Loreau 2001; Loreau et al. 2001; Bengtsson 2002; Lynch 2002; Aoki 2003). However, the positive correlation between diversity and resilience (and stability) already received criticisms in the 70s: May, in 1973 observed that an ecosystem depending on more species would be less stable (May 1988; Givnish et al. 1994; Andren et al. 1995; Ulanowicz 2003). Similarly it was shown how food chains of a longer length (with higher diversity) were less stable than shorter ones (May 1988; DeAngelis et al. 1989).

Nowadays there is consensus that a minimum number of species is essential for ecosystem functioning under constant conditions and that a larger number of species is probably necessary for maintaining the stability of ecosystem processes in changing environments (Ekschmitt & Griffiths 1998; Loreau et al. 2001).



**FIG. 2.** The relationship between stability of ecosystem function and diversity according to different hypotheses (Peterson et al. 1998).

### Functional Species Diversity

As mentioned above, the diversity–stability correlation could not be explained just by a mere taxonomic diversity, and ecosystem function and stability are more directly related to functional diversity (Hulot et al. 2000; McCann 2000).

The observation that higher diversity does not necessarily increase the functional stability of an ecosystem gave rise to the redundancy and insurance hypotheses proposing that ecological functions of different species may overlap and therefore influence the stability–diversity relationship (Figure 2b, c).

On the other hand, other hypotheses have attempted to explain the irregularities in the stability–diversity relationship by alternative mechanisms: for example how keystone species may emerge or be selected for, and how underlying ecological mechanisms constrain a direct stability–diversity relationship. In the following section, we will discuss niche differentiation, sampling effect, idiosyncrasy, and the effect of the metacommunity.

### Redundancy and Insurance

Ecosystems are resilient when ecological interactions reinforce one another and dampen disruptions. Such situations of “biological insurance” may arise due to compensation when a species with an ecological function similar to another species (redundant species) increases in abundance as the other declines (Holling 1996a; Naeem & Li 1998; Peterson et al. 1998). The observation that ecological functions of different species can overlap gave rise to new models. In 1981 Ehrlich et al. introduced the rivets model suggesting that ecological function is evenly partitioned among species, and that functional overlap of different species ensures that even if a species is removed, ecological function may persist because of the compensation of other species with similar functions (Figure 2b). This was

further developed into the “redundant species” hypothesis: ecological function is not distributed evenly among species, rather species can be divided in drivers (or determinants or keystone species) and passengers of the ecosystem. Ecosystem stability (as the probability of all species persisting) is enhanced if each important functional group of organisms comprises several ecologically equivalent species, each with different responses to environmental factors (Walker 1992). As a consequence, the removal of redundant species does not automatically imply loss of function (Griffiths et al. 2000; Briones & Raskin 2003). In this sense ecological redundancy has a positive effect as it enhances resilience. Therefore those groups with (too) few species deserve priority in conservation efforts. Besides, minor and unimportant species may emerge as keystone species in changed environments so that redundancy also provides an opportunity for further and future functions (adaptation) as well as a buffer from extinction (Walker 1995; Clarke & Warwick 1998; Peterson et al. 1998).

The insurance hypothesis proposes that biodiversity provides insurance or a buffer against environmental fluctuations, because different species respond differently to these fluctuations, leading to more predictable aggregate communities or ecosystem properties. In this sense, species that are redundant for an ecosystem at a given time may not be redundant at a later point in time (Naeem & Li 1998; Loreau et al. 2001; Hastings 2004; Loreau 2004). Nevertheless, this hypothesis does not infer that diversity actively promotes stability (Loreau 2004).

A further contribution to the functional diversity—resilience relationship was introduced with the functional—response diversity property that defines the diversity of responses to environmental change among species that contribute to the same ecosystem function (Elmqvist et al. 2003). Response diversity provides adaptive capacity in complex systems and, consequently, ecosystems with high response diversity increase the likelihood for renewal and reorganization into a desired state after disturbance (Elmqvist et al. 2003; Folke et al. 2004).

### Niche Differentiation, Sampling Effect, Idiosyncrasy, and Metacommunity Mechanisms

Niche differentiation and facilitation increase the performance of communities above expected performance of individual species in monoculture: this concept has been termed complementarity (Loreau et al. 2001; Naeem 2002).

According to the second mechanism, known as sampling effect, systems with higher community diversity are more likely to contain species which perform better (Andr n & Balandreau 1999; Loreau et al. 2001; Naeem 2002). Both niche differentiation and sampling effect therefore would affect the experimental results when measuring stability and resilience in function of a certain ecosystem function such as productivity, especially when short term effects (either in time or space) are under investigation (Loreau 2000).

The idiosyncratic model proposes that the degree of stability in a community depends idiosyncratically on which species are

present, suggesting that ecosystem function is contingent on the ecological history of a region and the evolutionary history of interacting species (Lawton et al. 1998). This model would imply that the relationship between structure and function is ecosystem-specific rather than universal (Peterson et al. 1998; Emmerson et al. 2001; Van Straalen 2002). However, if the effect of species diversity on ecosystem function is idiosyncratic, that is if species identity rather than diversity matters, it becomes very difficult to predict anything useful from measuring species richness (Figure 2) (Bengtsson 1998).

Curtis focuses on the surrounding environment of a local ecosystem of interest as the driving force in microbial community structure and termed it the metacommunity. The author applies the concepts of insurance, redundancy, sampling effect, and niche differentiation while defining each local community as a sample of the metacommunity, which has very different implications for the important determinants of resilience (Mouquet & Loreau 2002; Curtis & Sloan 2004; Leibold et al. 2004).

### Flux Models

An entirely different hypothesis in resilience theory was based on the idea that the ecosystems are characterized by fluxes of energy and nutrients that are continuously passing through the system. As a result, these fluxes could represent indicators for the quantification of system resilience (DeAngelis 1980; McCann 2000; Loreau 2001). DeAngelis reported how nutrient cycling models predicted an increase in resilience as the mean number of cycles that nutrient atoms make before leaving the system decreased (DeAngelis 1980). Resilience might depend on nutrient inputs, and nutrient limitation could stabilize the dynamics of the system in terms of local stability (DeAngelis et al. 1989). Similarly it was found that ecosystems generally develop towards increased productivity and biomass, a decreased productivity/biomass ratio and tighter nutrient cycling (Loreau 1998). However, in contrast to these models, Stone observed how resilience ultimately diminishes as productivity becomes large (Stone et al. 1996).

### Food Webs

A first step towards the formulation of hypotheses based on food webs is the realization that the complexity of whole ecological communities—on the basis of which Odum, Elton, and MacArthur formed their diversity–stability hypotheses—cannot manifest itself in experiments that focus on single trophic levels (McCann 2000). Pooling of species into “guilds,” or “functional groups” or the admission that there are “keystone species” and redundant species can also be seen as steps towards a hierarchical approach where species are ranked in a certain order according to their interdependency and where their interactions are described (Andr n & Balandreau 1999). Such a hierarchical approach, which at the same time links the general species diversity, their function and the fluxes, is the food web model

(De Ruiter et al. 1995; Huxel & McCann 1998; Van Straalen 2002). The stability of these food webs has been studied and several parameters have been proposed as indicators of stability or resilience of the ecosystem under investigation.

Most food web models relating to ecosystem resilience were based on the Lotka Volterra (1926) type, built considering each different trophic level constituting a food chain. The first type of food web, already mentioned by McArthur in 1955, was solely related to diversity: “as the number of links in the food web increases, the stability should increase.”

Increased complexity in the food web would lead to increased resilience and larger systems tend to be less stable, unless they are accompanied by an increasing relative number of paths, in accordance with the observation that longer food chains have a lower resilience (DeAngelis 1980; Walter 1980; May 1988; Martinez 1992; Cottingham & Carpenter 1994; Schwartz et al. 2000; Aoki 2003; Ulanowicz 2003).

These observations were grouped into a more general hypothesis, proposing that foodwebs with weak interaction strength present a higher level of connectance (Yodzis 1982; McCann 2000; Dunne et al. 2002; Kokkoris et al. 2002). Ulanowicz later proposed the term “ascendancy” as a measure derived from networks of trophic interactions and introduced the “ascendancy principle” according to which in the absence of major perturbations, ecosystems exhibit a tendency to increase in ascendancy, concluding that for a system to be stable two mutually exclusive attributes would be required: “system organization and system overhead, where overhead is determined by the disorganized, stochastic, inefficient, and incoherent aspects of a system’s activity” (Ulanowicz 2003).

## RESILIENCE IN PRACTICE

### Resilience in Microbial Systems

The first issue to deal with when applying the concept of resilience to a field situation or a laboratory experiment is the organism-ecosystem paradox, which is related to the “holist” versus “reductionist” perception of ecosystems (Andren et al. 1995; Holling 1996a, 1996b; Bengtsson 2002). Holistic approaches imply that an ecosystem is not merely the sum of its members and one should take into account for example all the interactions (even those unknown), the evolutionary aspect (history), the “outside environment,” the genetic potential etc. Even though it appears to be the most appropriate one, the holistic approach is not commonly used, for obvious practical reasons. Often a reductionist approach, i.e. to take the system apart and rebuild it from individual components, is more conveniently applied either in a constructive or a destructive manner. In the first case, communities are constructed with different levels of diversity by adding a varying number of species to the system (McGrady-Steed et al. 1997; Naeem & Li 1998; Griffiths et al. 2000; M ller et al. 2002; Van Straalen 2002). The destructive approach implies a reduction of diversity as a consequence of a specific treatment, for instance the application of a

certain perturbation to a soil sample followed by the monitoring of the effects on the microbial communities (Griffiths et al. 2000; Griffiths et al. 2001; Westergaard et al. 2001; Griffiths et al. 2004; Müller et al. 2004).

In order to circumvent the limitations that a reductionist approach could pose, other experimental set-ups have been proposed, such as the terrestrial model ecosystem or mesocosms in which a part of an ecosystem is isolated in such a way that there is as much control as possible on certain variables while the system is kept in its natural environment (Van Straalen 2002; Feris et al. 2004). Nonetheless, the issue of how scale influences outcome looms over microcosm experiments—can we extrapolate results to the whole ecosystem (McCann 2000)? And more generally, how is the experimental set-up of such experiments affecting the validity of the results in a larger context (Müller et al. 2002; Briones & Raskin 2003)? A new ambitious attempt to bridge the scale between field and laboratory perspectives is represented by the “Ecotron” project, in which multitrophic communities are built and monitored over long periods and under controllable conditions (McCann 2000).

The existing literature provides many examples of resilience studies in which a destructive approach is applied to the microbial systems under investigation. It is often the case that the quantification of resistance and/or resilience is based upon the engineering definition reported before: resistance is therefore calculated as the percentage of change from a control and resilience is quantified as the change of resistance over time.

For example Griffiths et al. 2000 and 2001 investigated the effects of different disturbances (fumigation followed by transient heat and persistent copper perturbations) on the functional stability (decomposition rate, nitrification, respiration etc.) in relation to microbial community composition measured in terms of bacterial biomass and phospholipidic fatty acids (PLFA) and denaturing gradient gel electrophoresis (DGGE) profiles in many different soils. Some resilience studies have focussed on the microbial communities and measured total microbial diversity or microbial community composition in relation to a disturbance in the soil (Loreau 2001; Lynch 2002; Grayston et al. 2004; Griffiths et al. 2004; Lynch et al. 2004; Griffiths et al. 2005). In some cases a positive link between biodiversity and resilience as well as faster recovery after transient stress could be observed (Griffiths et al. 2000; Griffiths et al. 2001; Müller et al. 2002; Ekelund et al. 2003; Feris et al. 2004). However, it appears that functional stability is more related to specific components within microbial communities that are possibly not yet fully understood (Andren et al. 1995; Griffiths et al. 2001; Griffiths et al. 2004; Heemsbergen et al. 2004). Similarly, other studies have also suggested that community structure rather than diversity would be a more appropriate parameter in the assessment of disturbance effects towards system function on soil populations (Westergaard et al. 2001). Moreover, the diversity-function relationship relies on the assumption that diversity, in terms of species richness, can be measured. Nevertheless it was already

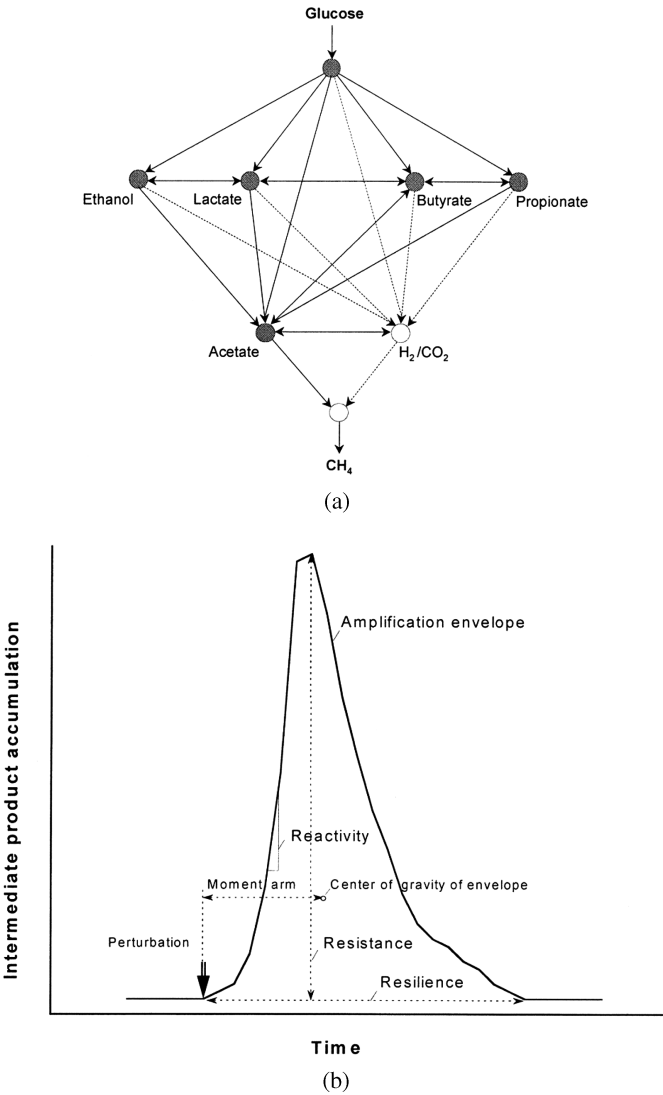
argued that severe difficulties affecting the measurements of species richness in soil protozoa and microorganisms represent a serious obstacle to any investigation (Ekschmitt & Griffiths 1998).

Yet new approaches are under development: a combination of biological and physical parameters to assess the effects of disturbances (such as metal contamination) on the biological and physical stability and resilience of soil has been recently proposed (Griffiths et al. 2005).

A remarkable long-term research was carried out in order to study microbial community dynamics in engineered ecosystems such as anaerobic methanogenic bioreactors. Using several molecular fingerprinting techniques, it was shown that these systems contain highly dynamic communities, which however maintained stable ecosystem function (measured as COD removal and pH of the effluent) over a period of almost two years when operated under constant conditions (Fernandez et al. 1999). When the same set-up was utilized to evaluate the response of the system in terms of functional stability and community structure in reaction to a disturbance (glucose shock) very interesting outcomes emerged. Two sets of bioreactor communities were established that differed in their respective methanogenic populations with one set being characterized by lower species diversity than the other (in Figure 3A an example of the multiple substrate routes within methanogenic communities is given). The two systems reacted differently in terms of accumulation of intermediates in response to the perturbation and, in particular, the community in the reactor with lower diversity was able to channel substrate through parallel pathways that eventually enabled a faster recovery, whereas in the more diverse community the serial substrate processing required a longer recovery. This observation seems to support the hypothesis that a network of multiple routes for substrate flow confers greater functional stability (Hashsham et al. 2000). Moreover the evaluation of population dynamics revealed that the less diverse but more functionally stable community was less stable in terms of community structure or, in other words, more flexible. Also, some numerically minor members of the community responded to the perturbation and in general a pronounced shift in relative abundance of fermentative bacteria was observed.

This implies that functional stability does not necessarily correlate with stability in community structure and even suggests that a less flexible or more “stable” microbial community structure results in poor functional stability following a significant perturbation. This may be because organisms that are dominant under steady-state conditions are not necessarily the organisms best adapted to perturbed conditions (Fernandez et al. 2000).

The pattern of metabolite accumulation in response to the perturbation was utilized for the quantification of various parameters including resistance, resilience, and reactivity for each product, according to a new stability parameter: “moment of amplification envelope” as shown in Figure 3B. The two main parameters obtained from the envelope depicted in Figure 3B are



**FIG. 3.** Anaerobic food chain as a network of substrate flow through a methanogenic community (A) and ecological parameters of functional stability (B). Reprinted with permission (Hashsham et al. 2000).

resistance and resilience, where resistance of a community with respect to an intermediate product was defined as the maximum accumulation of the product and is a measure of the buffering capacity of the community with respect to the corresponding intermediate product. Resilience was defined as the time taken by the accumulated intermediate product to return to its referential state.

From these studies we can therefore conclude that those systems characterized by lower community diversity but higher flexibility, in terms of parallel flow-of-substrate pathways and population dynamics, are more resilient towards a perturbation. In addition, ecosystem stability would be the outcome of functional redundancy, which is ensured by the presence of a reservoir of species able to perform the same ecological function (Briones & Raskin 2003).

**Resilience and Environmental Management**

Resilience is more than the sum of processes taking place in a defined system; it is related to the mechanistic understanding of ecosystem behavior under changing conditions. In the sense of environmental policy making and management, as already mentioned in the introduction, resilience does not always have a positive connotation and is thus not necessarily desirable.

If we look at a hypothetical environmental system after a certain perturbation has occurred, we can identify a set of six possible scenarios that could characterise the new system (Figure 4). The different scenarios also imply varying degrees of management effort (or input) that should be applied in order to reach the desired situation (in this case we assume that the desired situation is “clean”) is related to the resilience of the system under investigation.

If we assume that a pristine (unpolluted) aquifer becomes polluted, one of the possible approaches to face this new and undesirable situation could be to investigate whether bacteria are present that could actively degrade and remove a certain harmful pollutant: in this case biodegradation could be a tool for remediation or natural attenuation. If this is indeed the case, the system could be returning to the original state once the pollutant is being removed by the indigenous microorganisms (case A in Figure 4). Also, because the previous stability domain (or valley of Figure 1) will be reached again, the system proved to be ecologically resilient (case A) towards that particular perturbation (pollution). In ecological terms, the system was highly resilient toward a specific disturbance and it is therefore moving back to its original equilibrium.

However, the same result in terms of pollution removal could have been reached via a totally different route, assuming that after the disturbance occurred, the same system has reached a

Resilience of a system after a perturbation	System moves towards	Characteristics of the system in equilibrium	Management input to reach desired quality in certain time
High	New equilibrium	Clean (desired)	A ←
		Polluted (undesired)	B ←
	Previous equilibrium	Clean (desired)	C ←
Low	New equilibrium	Clean (desired)	D ←
		Polluted (undesired)	E ←
	Previous equilibrium	Clean (desired)	F ←

**FIG. 4.** Assessment of a hypothetical system after a perturbation has occurred. The resilience of the system is related to the shape of the curve as depicted in Figure 1. Resilience changes as the characteristics of a system change. When taking into account that a disturbance may have reshaped the original curve, or the system may have moved to another attraction domain, it can occur that the resilience of a system before and after the perturbation are not related anymore.

new equilibrium that is profoundly different from the previous (pristine) environment (case D) and although “clean” it could now for example host different species, or new food webs could be established and novel interactions might have developed. In this case, the final goal has been met as in the previous case but a new environment different from the starting one has developed. Ecological theory would then say that the system was not resilient because a novel stable equilibrium that is drastically different from the original one (the system has moved to another domain of attraction) was reached.

Similarly, if we assume that the system after the perturbation is moving back towards its original equilibrium, which therefore is a clean situation, scenario C and F are also possible. The resilience of the current system may be high or low, nevertheless the goals for clean-up are being met.

A comparison of the clean scenarios that a system could reach when it has high resilience (A and C) with the clean scenarios of a system with low resilience (D and F) suggests that management efforts are generally more needed for those systems with low resilience in order to speed up the return to the equilibrium after the displacement. Also, such efforts should aim at keeping those systems within the boundaries of the valley of Figure 1, as low resilience implies higher vulnerability.

In contrast, for cases B and E, where a new polluted equilibrium has developed, the situation in which the system has high resilience (B) is less desirable than the one with low resilience (E) because higher effort is needed to bring about changes to a system with high resilience. The same consideration would apply for scenarios A and D if the aims were directed towards bringing the system back to all its original values as before the perturbation happened.

It is important to realize that it is hardly possible to assess the degree of resilience towards external disturbances of a system before a perturbation actually occurred, since the original conditions and the size of the perturbation applied are generally not known.

Concluding, according to the hypothetical system of Figure 4 it becomes evident that resilience alone is not suitable as the driving parameter on the basis of which the management of a polluted system is developed. High or low resilience could both be desirable for restoration of a polluted aquifer depending on the initial conditions and on the very system under investigation

## RESILIENCE IN MICROBIAL ECOLOGY: CONSIDERATIONS

It is clear that the limited number of resilience studies addressing soil ecosystems and including the microbiota makes it difficult to choose a universal method for measuring resilience in these ecosystems. Already within the soil, a distinction between top soil or subsoil studies can be made: top soil processes are more related to the above ground ecosystem, and the interest is often restricted to the main element cycles of C, N, P, and S. Fluxes of these elements or overall rates of microbial

activity have been used to study the influence of the microbial community on overall ecosystem processes (Nannipieri et al. 2003; Lynch et al. 2004). However in subsoil and aquifers, the main concern when evaluating a property like resilience, is the self-purifying ability (by natural attenuation or biodegradation) of the soil after pollution has occurred. In this case concentrations of residual pollutant are generally the most important target parameter (Curtis & Sloan 2004).

When translating existing hypotheses to soil microbial communities it is important to realize that the above ground effects of biodiversity on ecosystem functioning may not be the same as those relationships occurring below ground, due to some fundamental differences in the physical structure of above- and below ground systems (Lawton et al. 1998; Griffiths et al. 2000; Grime 2003). Even though significant effects of species diversity on soil resilience have been demonstrated, the experiments were focused on effects of plant diversity on primary production and nutrient retention. The reason these experiments often failed to detect significant effects on below-ground decomposition processes could be that these processes are under microbial control (Loreau 2001).

## Choice of Strategy

The first point to be considered when designing experiments aimed at studying resilience is how the different practical choices and theoretical assumptions will affect the applicability of the results. Even with all the presently available techniques a reductionist approach is often applied for studying resilience in microbial ecosystems: a simplified community in an engineered closed system like a reactor with full control of the variables or a single species or (functional) group study. When using such an approach, the resulting communities have unrealistically low species diversity and only culturable organisms can be used (Müller et al. 2002; Briones & Raskin 2003). Also with enrichment techniques, microbial communities could be unrepresentative of in situ community structure and again culturable species will be selected for.

Even though it is difficult to extrapolate results obtained in these experiments to whole ecosystem dynamics, with the advent of functional ecogenomic strategies that aim at unravelling genetic and metabolic diversity and activity of microbial populations in metacommunities, the approaches may take a new turn towards more integrative (or holistic) approaches: a challenging perspective at the moment (Daniel 2004; Eysers et al. 2004).

## Choice of Parameters and Reference (Control)

Another aspect that greatly influences the outcome of a study is the choice of monitored parameters and reference system. Probably the most important issue in any resilience study is the determination of the base line (Orwin & Wardle 2004). This aspect is also linked to the choice of which measurable parameters to apply in the whole study (Duelli & Obrist 2003). How can the stability of an undisturbed system be determined?



What is an undisturbed system (Van Straalen 2002)? Each choice will largely depend on the human interest in the function of the specific ecosystem: e.g. in the case of arable land, plant productivity parameters are often taken along or in the case of a polluted aquifer the central question would be how harmful the contaminants are for both the environment and the population.

In many cases the indicators and parameters applied are chosen on the basis of the very ecosystem under observation and the scale and the perturbation that is being considered (Peterson et al. 1998). The stability of a system is therefore also related to this choice, as it was shown by Fernandez: a long-term stability in reactor performance (chemical parameters) was not related to stability in the microbial community (Fernandez et al. 1999; Fernandez et al. 2000; Hashsham et al. 2000).

Also the methodology may influence the final results: it has been shown that already the choice of DNA extraction methods can produce inconsistent results (Westergaard et al. 2001; Ranjard et al. 2003).

Moreover, the stability of a system is also related to its history. For an organism to grow it may be necessary that another organism has modified the environment previously (Andren et al. 1999). The effect of a new disturbance on the system also depends on previous events, their duration and their specificity: after a transient disturbance a system could have returned to its former state, whereas a permanent disturbance could have resulted already in a new state (Müller et al. 2002). When determining reference points, these "historical" characteristics are inadvertently taken along and may have an influence on the outcome of the study.

### Cultivation vs. Molecular Approaches

It should also be pointed out that there are many practical difficulties in studying a microbial ecosystem. It is generally known that many soil microorganisms cannot be cultivated, a large fraction of soil bacteria remains undescribed and as Griffith already mentioned, neither for bacteria, fungi nor for protozoa, we are able to link the large taxonomic diversity in soil to the functioning of microbial ecosystems (Griffiths et al. 2000; Palumbo et al. 2004).

With the advent of molecular techniques a whole range of new options have become available for studying microbial ecosystem structures *in situ*. Lynch and Nannipieri presented a variety of options, including the analysis of molecular taxonomic markers, mRNA, and enzyme activity as the accumulated pool of a biological reaction in the soil which can again be measured by more precise chemical methods (Nannipieri et al. 2003; Lynch et al. 2004). Newly emerging techniques such as stable isotope probing (SIP) and microautoradiography–fluorescent *in situ* hybridization (MAR-FISH) or catalyzed reporter deposition–fluorescent *in situ* hybridization (CARD-FISH), that are specifically aimed at linking identity to function, can also help overcome some of the problems (Hugenholtz et al. 1998; Rodríguez-Valera 2002; Daniel 2004; Eysers et al. 2004; Guichard et al. 2004;

Lynch et al. 2004; Riesenfeld et al. 2004; Streit & Schmitz 2004; Hartmann et al. 2005; Liu & Zhu 2005).

### Catastrophic Shifts, Adaptation and Evolution

An additional dimension with respect to the role of microbial diversity in natural systems is related to the microbial adaptations to spatial and temporal variations in the environment: bacteria live in a dormant state until conditions become favorable, (supporting the insurance hypothesis) (Loreau et al. 2001). Real ecosystems are driven and shaped largely by stochastic events and for these systems the spatial distributions of species and their interactions are likely to be governed by chance more than anything else (Scheffer et al. 2001; Scheffer & Carpenter 2003). Furthermore, because deterministic physical processes could hardly describe such systems, the concept of resilience becomes almost meaningless: how could perturbed populations return to some fundamental dynamic behavior (equilibrium or periodic oscillation) if there is no deterministic regulation (Stone et al. 1996)? Therefore, most of the classical equilibrium approaches may be inadequate to understand stability properties such as resilience and resistance at ecosystem level. New approaches should be developed that take into account the dynamics of diversity and the potential for adaptation through phenotypic plasticity, evolutionary changes, and species replacement (Loreau et al. 2001). Indicators of adaptive capacity should address the ability of the ecosystem to cope with change. In biotic systems, adaptive capacity is related to genetic diversity (because the rate of evolution is proportional to the variability that selective forces can work on), biodiversity (for example, portfolio effects), and the heterogeneity of landscape mosaics (Peterson et al. 1998; Loreau 2000). By using functional ecogenomics approaches different parameters are taken into account, including a certain measure of genetic adaptive capacities (Riesenfeld et al. 2004; Streit & Schmitz 2004; Stauffer et al. 2005). Experiments dedicated at studying the relationships between these new parameters and ecosystem dynamics may lead to reformulation of existing hypotheses or improved formulation of existing ones.

### SUMMARY

Nowadays environmental managers and policy makers frequently adopt the term resilience when discussing environmental protection strategies. However, the concept of resilience is not well defined and this is especially true for ecosystems governed by microbial interactions.

A review of the literature of the last decade shows that the concept of resilience in systems ecology has been applied in numerous studies over the past fifty years: a variety of definitions have been formulated and a large number of experimental approaches to test them have been proposed. Only a few studies have investigated the resilience of subsoil and groundwater ecosystems including the microbial community structure and function. Moreover, the necessary simplification required to approach such studies has inevitably brought a reduction of the

microbial community into one (bacteria) or few functional groups and very few studies have described stability and resilience in a solely microbial ecosystem.

Resilience is the outcome of more than merely the sum of the processes taking place; it is related to the mechanistic understanding of ecosystem behavior under changing conditions. To study resilience of an ecosystem it is therefore necessary to create a true full picture of that system and this may also include its history and possible future genetic capacity. A combination of techniques that include the overall biogeochemical processes, microbial activity, and taxonomic or genetic diversity will help linking the microbial structure and diversity of a soil to its function.

In the sense of environmental protection, resilience should not be confused with other terms like natural attenuation or biodegradation as it does not always have a positive connotation or it is not necessarily desirable. When setting goals for environmental protection, it is important to use well defined terms that clearly point out what is the final goal with respect to the specific system under investigation and the desirable end result of the undertaken action.

In this paper we aim at summarizing the current definitions of resilience in systems ecology and how they are applied in practice, with special attention to systems governed by microbial processes, as is the case for subsoil and groundwater ecosystems. This review has led to some reflection on the suitability of the term "resilience" as a general goal in environmental policies.

While scientists are gaining new tools and applying novel methodologies to study microbial systems at different scales and resolution, policymakers and managers should be aware of gaps and open questions in theories and therefore apply the term "resilience" with caution, without confusing it with generally accepted and well defined concepts like biodegradation or natural attenuation. As long as there is no real consensus on which are the parameters of resilience in an ecosystem, the only way one could evaluate the degree of resilience of a system is to study the "before" and "after" situations. The outcome of a study will always depend on the ecosystem under consideration, the choice of parameters to measure and the choice of functions or set of characteristics taken into account at the starting situation.

With the advance of biomolecular techniques scientists have obtained new tools to investigate these systems in more detail and with greater resolution. It is time therefore to revisit the existing concepts and hypotheses and discuss their applicability to ecosystems ruled by microbial processes. A new challenge lies ahead for microbial ecologists: to formulate improved hypotheses on resilience sustained by novel results and advanced methodologies, allowing for more holistic approaches.

## ACKNOWLEDGEMENTS

We acknowledge the Netherlands Organization for Scientific Research (NWO) for funding in the framework of TRIAS project

835.80.007, resilience of the groundwater ecosystem in reaction to anthropogenic disturbances.

## REFERENCES

- Andr n, O., and Balandreau, J. 1999. Biodiversity and soil functioning—From black box to can of worms? *Applied Soil Ecology* 13, 105–108.
- Andr n, O., Bengtsson, J., and Clarholm, M. 1995. Biodiversity and species redundancy among litter decomposers. In: The significance and regulation of soil biodiversity, Kluwer Academic Publishers, pp. 141–151.
- Andr n, O., Brussaard, L., and Clarholm, M. 1999. Soil organism influence on ecosystem-level processes—Bypassing the ecological hierarchy? *Applied Soil Ecology* 11, 177–188.
- Aoki, I. 2003. Diversity-productivity-stability relationship in freshwater ecosystems: Whole-systemic view of all trophic levels. *Ecological Research* 18, 397–404.
- Bengtsson, J. 1998. Which species? What kind of diversity? Which ecosystem function? Some problems in studies of relations between biodiversity and ecosystem function. *Applied Soil Ecology* 10, 191–199.
- Bengtsson, J. 2002. Disturbance and resilience in soil animal communities. *European Journal of Soil Biology* 38, 119–125.
- Briones, A., and Raskin, L. 2003. Diversity and dynamics of microbial communities in engineered environments and their implications for process stability. *Current Opinion in Biotechnology* 14, 270–276.
- Carpenter, S., Walker, B., Anderies, J.M., and Abel, N. 2001. From Metaphor to Measurement: Resilience of What to What? *Ecosystems* 4, 765–781.
- Clarke, K.R., and Warwick, R.M. 1998. Quantifying structural redundancy in ecological communities. *Oecologia* 113, 278–289.
- Cottingham, K.L., and Carpenter, S.R. 1994. Predictive indices of ecosystem resilience in models of north temperate lakes. *Ecology* 75, 2127–2138.
- Curtis, T.P., and Sloan, W.T. 2004. Prokaryotic diversity and its limits: Microbial community structure in nature and implications for microbial ecology. *Current Opinion in Microbiology* 7, 221–226.
- Daniel, R. 2004. The soil metagenome—A rich resource for the discovery of novel natural products. *Current Opinion in Biotechnology* 15, 199–204.
- De Ruiter, P.C., Neutel, A.M., and Moore, J.C. 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science* 269, 1257–1260.
- DeAngelis, D.L. 1980. Energy flow, nutrient and ecosystem resilience. *Ecology* 61, 764–771.
- DeAngelis, D.L., Mulholland, P.J., Palumbo, A.V., Steinman, A.D., Huston, M.A., and Elwood, J.W. 1989. Nutrient dynamics and food-web stability. *Annual Review of Ecology and Systematics* 20, 71–95.
- Duelli, P., and Obst, M.K. 2003. Biodiversity indicators: The choice of values and measures. *Agriculture, Ecosystems and Environment* 98, 87–98.
- Dunne, J.A., Williams, R.J., and Martinez, N.D. 2002. Food-web structure and network theory: The role of connectance and size. *Proceedings of the National Academy of Sciences of the United States of America* 99, 12917.
- Ekelund, F., Olsson, S., and Johansen, A. 2003. Changes in the succession and diversity of protozoan and microbial populations in soil spiked with a range of copper concentrations. *Soil Biology & Biochemistry* 35, 1507–1516.
- Ekschmitt, K., and Griffiths, B.S. 1998. Soil biodiversity and its implications for ecosystem functioning in a heterogeneous and variable environment. *Applied Soil Ecology* 10, 201–215.
- Elmqvist, T., Folke, C., Nystr m, M., Peterson, G., Bengtsson, J., et al. 2003. Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment* 1, 488–494.
- Elton, C.S. 1958. The ecology of invasions by animals and plants. London: Methuen.
- Emmerson, M.C., M.S., C.E., D.M. P., D.R. 2001. Consistent patterns and the idiosyncratic effects of biodiversity in marine ecosystems. *Nature* 411, 73–77.
- Eyers, L., George, I., Schuler, L., Stenuit, B., Agathos, S.N., and El Fantroussi, S. 2004. Environmental genomics: Exploring the unmined richness of microbes

- to degrade xenobiotics. *Applied Microbiology and Biotechnology* 66, 123–130.
- Feris, K.P., Ramsey, P.W., Rillig, M., Gannon, J.E., Holben, W.E., and Moore, J.N. 2004. Determining rates of change and evaluating group-level resiliency differences in hyporheic microbial communities in response to fluvial heavy-metal deposition. *Applied and Environmental Microbiology* 70, 4756–4765.
- Fernandez, A., Huang, S., Seston, S., Xing, J., Hickey, R. et al. 1999. How stable is stable? Function versus community composition. *Applied and Environmental Microbiology* 65, 3697–3704.
- Fernandez, A.S., Hashsham, S.A., Dollhopf, S.L., Raskin, L., Glagoleva, O., et al. 2000. Flexible community structure correlates with stable community function in methanogenic bioreactor communities perturbed by glucose. *Applied and Environmental Microbiology* 66, 4058–4067.
- Folke, C., Carpenter, S., Elmqvist, T., Gunderson, L., Holling, C.S., and Walker, B. 2002. Resilience and sustainable development: Building adaptive capacity in a world of transformations. *Ambio* 31, 437–440.
- Folke, C., Elmqvist, T., Carpenter, S., Walker, B., Scheffer, M. et al. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics* 35, 557–581.
- Givnish, T.J., Tilman, D., Downing, J.A., and Wedin, D.A. 1994. Does diversity beget stability? *Nature* 371, 113–114.
- Grayston, S.J., Campbell, C.D., Millard, P., Mawdsley, J.L., Clegg, C.D. et al. 2004. Assessing shifts in microbial community structure across a range of grasslands of differing management intensity using CLPP, PLFA and community DNA techniques. *Applied Soil Ecology* 25, 63–84.
- Griffiths, B.S., Hallett, P., Kuan, H., Pitkin, Y., and Aitken, M. 2005. Biological and physical resilience of soil amended with heavy metal-contaminated sewage sludge. *European Journal of Soil Science* 56, 197–205.
- Griffiths, B.S., Kuan, H.L., Ritz, K., Glover, L.A., McCaig, A.E., and Fenwick, C. 2004. The relationship between microbial community structure and functional stability, tested experimentally in an upland pasture soil. *Microbial Ecology* 47, 104–113.
- Griffiths, B.S., Ritz, K., Bardgett, R.D., Cook, R., Christensen, S., et al. 2000. Ecosystem response of pasture soil communities to fumigation-induced microbial diversity reductions: An examination of the biodiversity-ecosystem function relationship. *Oikos* 90, 279–294.
- Griffiths, B.S., Ritz, K., Wheatley, R., Kuan, H.L., Boag, B. et al. 2001. An examination of the biodiversity-ecosystem function relationship in arable soil microbial communities. *Soil Biology and Biochemistry* 33, 1713–1722.
- Grime, P. 2003. Plants hold the key. Ecosystem in a changing world. *Biologist* 50, 87–91.
- Guichard, F., Levin, S.A., Hastings, A., and Siegel, D. 2004. Toward a dynamic metacommunity approach to marine reserve theory. *BioScience* 54, 1003–1011.
- Gunderson, L.H. 2000. Ecological resilience—In theory and application. *Annual Review of Ecology and Systematics* 31, 425–439.
- Häggblom, M.M., Knight, V.K., and Kerkhof, L.J. 2000. Anaerobic decomposition of halogenated aromatic compounds. *Environmental Pollution* 107, 199–207.
- Hartmann, M., Kölliker, R., Widmer, F., and Frey, B. 2005. Semi-automated genetic analyses of soil microbial communities: Comparison of T-RFLP and RISA based on descriptive and discriminative statistical approaches. *Journal of Microbiological Methods* 61, 349–360.
- Hashsham, S.A., Fernandez, A.S., Dollhopf, S.L., Dazzo, F.B., Hickey, R.F. et al. 2000. Parallel processing of substrate correlates with greater functional stability in methanogenic bioreactor communities perturbed by glucose. *Applied and Environmental Microbiology* 66, 4050–4057.
- Hastings, A. 2004. Transients: The key to long-term ecological understanding? *Trends in Ecology and Evolution* 19, 39–45.
- Heemsbergen, D.A., Berg, M.P., Verhoef, H.A., Heemsbergen, D.A., Van Hal, J.R. et al. 2004. Biodiversity effects on soil processes explained by interspecific functional dissimilarity. *Science* 306, 1019–1020.
- Holling, C.S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4, 1–23.
- Holling, C.S. 1996a. Engineering resilience versus ecological resilience. National Academy Press, Washington, DC.
- Holling, C.S. 1996b. Surprise for science, resilience for ecosystems, and incentives for people. *Ecological Applications* 6, 733–735.
- Hugenholtz, P., Goebel, B.M., and Pace, N.R. 1998. Impact of culture-independent studies on the emerging phylogenetic view of bacterial diversity. *Journal of Bacteriology* 180, 4765–4774.
- Hulot, F.D., Lacroix, G., Lescher-Moutoué, F., and Loreau, M. 2000. Functional diversity governs ecosystem response to nutrient enrichment. *Nature* 405, 340–344.
- Huxel, G.R., and McCann, K. 1998. Food web stability: The influence of trophic flows across habitats. *American Naturalist* 152, 460–469.
- Johnson, J.L., and Wiechelt, S.A. 2004. Introduction to the special issue on resilience. *Substance Use and Misuse* 39, 657–670.
- Kokkoris, G.D., Jansen, V.A.A., Loreau, M., and Troumbis, A.Y. 2002. Variability in interaction strength and implications for biodiversity. *Journal of Animal Ecology* 71, 362–371.
- Lal, R. 1997. Degradation and resilience of soils. *Phil. Trans. R. Lond. B* 352, 997–1010.
- Lawton, J.H., Naem S., Thompson, L.J., Hector, A., Crawley, M.J. et al. 1998. Biodiversity and ecosystem function: Getting the Ecotron experiment in its correct context. *Functional Ecology* 12, 848–853.
- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M. et al. 2004. The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters* 7, 601–613.
- Liu, W.T., and Zhu, L. 2005. Environmental microbiology-on-a-chip and its future impacts. *Trends in Biotechnology* 23, 174–179.
- Loreau, M. 1998. Biodiversity and ecosystem functioning: A mechanistic model. *Proceedings of the National Academy of Sciences of the United States of America* 95, 5632–5636.
- Loreau, M. 2000. Biodiversity and ecosystem functioning: Recent theoretical advances. *Oikos* 91, 3–17.
- Loreau, M. 2001. Microbial diversity, producer-decomposer interactions and ecosystem processes: A theoretical model. *Proceedings of the Royal Society of London—Biological Sciences* 268, 303–309.
- Loreau, M. 2004. Does functional redundancy exist? *Oikos* 104, 606–611.
- Loreau, M., S.N., P.I., J.B., J.P.G., et al. 2001. Ecology: Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science* 294, 804–808.
- Lynch, J.M. 2002. Resilience of the rhizosphere to anthropogenic disturbance. *Biodegradation* 13, 21–27.
- Lynch, J.M., Benedetti, A., Insam, H., Nuti, M.P., Smalla, K. et al. 2004. Microbial diversity in soil: Ecological theories, the contribution of molecular techniques and the impact of transgenic plants and transgenic microorganisms. *Biology and Fertility of Soils* 40, 363–385.
- MacArthur, R. 1955. Fluctuations of Animal Populations and a Measure of Community Stability. *Ecology* 36, 533–536.
- Martinez, N.D. 1992. Constant connectance in community food webs. *American Naturalist* 139, 1208–1218.
- May, R.M. 1988. How many species are there on earth? *Science* 241, 1441–1449.
- McCann, K.S. 2000. The diversity-stability debate. *Nature* 405, 228–233.
- McGrady-Steed, J., Harris, P.M., and Morin, P.J. 1997. Biodiversity regulates ecosystem predictability. *Letters to Nature* 390, 162–165.
- Mouquet, N., and Loreau, M. 2002. Coexistence in metacommunities: The regional similarity hypothesis. *American Naturalist* 159, 420–426.
- Müller, A.K., Westergaard, K., Sørensen, S.J., and Christensen, S. 2002. The diversity and function of soil microbial communities exposed to different disturbances. *Microbial Ecology* 44, 49–58.
- Naem, S. 2002. Ecosystem consequences of biodiversity loss: The evolution of a paradigm. *Ecology* 83, 1537–1552.
- Naem, S., and Li, S. 1998. A more reliable design for biodiversity study? *Nature* 394, 30.
- Nannipieri, P., Ascher, J., Ceccherini, M.T., Landi, L., Pietramellara, G., and Renella, G. 2003. Microbial diversity and soil functions. *European Journal of Soil Science* 54, 655–670.

- Orwin, K.H., and Wardle, D.A. 2004. New indices for quantifying the resistance and resilience of soil biota to exogenous disturbances. *Soil Biology and Biochemistry* 36, 1907–1912.
- Palumbo, A.V., Schryver, J.C., Fields, M.W., Bagwell, C.E., Zhou, J.Z. et al. 2004. Coupling of functional gene diversity and geochemical data from environmental samples. *Applied and Environmental Microbiology* 70, 6525–6534.
- Peterson, G., Craig, R.A., and Holling, C.S. 1998. Original articles: Ecological resilience, biodiversity, and scale. *Ecosystems* 1, 6–18.
- Ranjard, L., Lejon, D.P.H., Mougel, C., Chaussod, R., Schehrer, L., and Merdinoglu, D. 2003. Sampling strategy in molecular microbial ecology: Influence of soil sample size on DNA fingerprinting analysis of fungal and bacterial communities. *Environmental Microbiology* 5, 1111–1120.
- Riesenfeld, C.S., Schloss, P.D., and Handelsman, J. 2004. Metagenomics: Genomic analysis of microbial communities. *Annual Review of Genetics* 38, 525–552.
- Rodríguez-Valera, F. 2002. Approaches to prokaryotic biodiversity: A population genetics perspective. *Environmental Microbiology* 4, 628–633.
- Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., and Walker, B. 2001. Catastrophic shifts in ecosystems. *Nature* 413, 591–596.
- Scheffer, M., and Carpenter, S.R. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology and Evolution* 18, 648–656.
- Schwartz, M.W., Brigham, C.A., Hoeksema, J.D., Lyons, K.G., Mills, M.H., and Van Mantgem, P.J. 2000. Linking biodiversity to ecosystem function: Implications for conservation ecology. *Oecologia* 122, 297–305.
- Stauffer, D., Kunwar, A., and Chowdhury, D. 2005. Evolutionary ecology in silico: Evolving food webs, migrating population and speciation. *Physica A: Statistical Mechanics and its Applications* 352, 202–215.
- Stone, L., Gabric, A., and Berman, T. 1996. Ecosystem resilience, stability, and productivity: Seeking a relationship. *American Naturalist* 148, 892–903.
- Streit, W.R., and Schmitz, R.A. 2004. Metagenomics—The key to the uncultured microbes. *Current Opinion in Microbiology* 7, 492–498.
- Tilman, D., and Downing, J.A. 1994. Biodiversity and stability in grasslands. *Nature* 367, 363–365.
- Ulanowicz, R.E. 2003. Some steps toward a central theory of ecosystem dynamics. *Computational Biology and Chemistry* 27, 523–530.
- Van Straalen, N.M. 2002. Assessment of soil contamination—A functional perspective. *Biodegradation* 13, 41–52.
- Walker, B. 1995. Conserving biological diversity through ecosystem resilience. *Conservation Biology* 9, 747–752.
- Walker, B., Anderies, J., Abel, N., Carpenter, S., Peterson, G.D. et al. 2002. Resilience management in social-ecological systems: A working hypothesis for a participatory approach. *Conservation Ecology* 6.
- Walker, B.H. 1992. Biodiversity and Ecological Redundancy. *Conservation Biology* 6, 18–23.
- Waller, M.A. 2001. Resilience in ecosystemic context: Evolution of the concept. *American Journal of Orthopsychiatry* 71, 290–297.
- Walter, G.G. 1980. Stability and structure of compartmental models of ecosystems. *Mathematical Biosciences* 51, 1–10.
- Westergaard, K., Müller, A.K., Christensen, S., Bloem, J., and Sørensen, S.J. 2001. The effect of Tylosin as a Disturbance on the Soil Microbial Communities. *Soil Biology & Biochemistry* 33, 2061–2071.
- Yodzis, P. 1982. The compartmentation of real and assembled ecosystems. *American Naturalist* 120, 551–570.